

Our grooming cousins : providing the link to declarative signalling?

Autor(en): **Pika, Simone**

Objektyp: **Article**

Zeitschrift: **Studies in Communication Sciences : journal of the Swiss Association of Communication and Media Research**

Band (Jahr): **9 (2009)**

Heft 1

PDF erstellt am: **23.07.2024**

Persistenter Link: <https://doi.org/10.5169/seals-791039>

Nutzungsbedingungen

Die ETH-Bibliothek ist Anbieterin der digitalisierten Zeitschriften. Sie besitzt keine Urheberrechte an den Inhalten der Zeitschriften. Die Rechte liegen in der Regel bei den Herausgebern.

Die auf der Plattform e-periodica veröffentlichten Dokumente stehen für nicht-kommerzielle Zwecke in Lehre und Forschung sowie für die private Nutzung frei zur Verfügung. Einzelne Dateien oder Ausdrucke aus diesem Angebot können zusammen mit diesen Nutzungsbedingungen und den korrekten Herkunftsbezeichnungen weitergegeben werden.

Das Veröffentlichen von Bildern in Print- und Online-Publikationen ist nur mit vorheriger Genehmigung der Rechteinhaber erlaubt. Die systematische Speicherung von Teilen des elektronischen Angebots auf anderen Servern bedarf ebenfalls des schriftlichen Einverständnisses der Rechteinhaber.

Haftungsausschluss

Alle Angaben erfolgen ohne Gewähr für Vollständigkeit oder Richtigkeit. Es wird keine Haftung übernommen für Schäden durch die Verwendung von Informationen aus diesem Online-Angebot oder durch das Fehlen von Informationen. Dies gilt auch für Inhalte Dritter, die über dieses Angebot zugänglich sind.

SIMONE PIKA*

OUR GROOMING COUSINS: PROVIDING THE LINK TO DECLARATIVE SIGNALLING?¹

Around the globe, human speech is frequently accompanied by movements of the arms and hands that are termed gestures. Recently the study of gestures has received tremendous research attention and provided evidence that gestures are used functionally in ways very similar to speech, that is symbolically, referentially, and based on intersubjectively learned and shared social conventions. Our closest living relatives, the great apes also use gestures in their natural communication. These gestures resemble those of pre-linguistic human children in some important ways, but they also share two important components that make them crucially different from human deictic and symbolic gestures: They are most frequently used in dyadic interactions and seem to be performed exclusively for imperative purposes to request actions from others. Pre-linguistic human children however also use gestures declaratively to direct the attention of others to an outside object or event, simply to share interest in it or comment on it; an ability which might have triggered the onset of speech. Declarative signalling is probably linked with an increased level of intersubjectivity that enables humans to understand other people as intentional agents with whom they may share experience. Focusing on its evolutionary origins, declarative signalling might have been derived from the need to create a new medium for social bonding triggered by an increase of group size, superseding grooming as a servicing tool for social relationships.

Keywords: communication, gestures, chimpanzees, cognition.

* University of Manchester, School of Psychological Sciences, simone.pika@manchester.ac.uk

¹ I am grateful to R. I. M. Dunbar, whose work and hypotheses inspired this paper. For comments on an earlier draft and lively discussions, I would like to thank T. Racine, D. Leavens and S. Reynolds.

1. Introduction

Animal communication has received tremendous research attention in recent years from scientists in a variety of disciplines such as psychology, neurobiology, ethology, behavioural ecology and evolutionary biology. In most definitions of the term, the fundamental building blocks of communication are signals, which show two crucial characteristics: a) they convey information in the form of energy or matter, and b) elicit a behavioural response in the receiver (Markl 1983, 1987). The diversity of animal signals is manifold, ranging from visual signals such as bright plumages of birds and antlers of deer, to auditory signals such as calls of frogs and crickets, to olfactory signals such as pheromones released by moths, ants and many other insects, to tactile signals found in many mammal species.

Researchers intrigued by the puzzle of language evolution focus quite naturally on the complexity of signal structure and signal usage of vocalizations in our closest living relatives, the non-human primates (hereafter primates). Recent studies suggest that primates possess rudimentary abilities with respect to three key features essential for human language, the ability to *a*) learn and modify calls (e.g., Mitani et al. 1992; Crockford et al. 2004), *b*) combine calls syntactically (Arnold & Zuberbühler 2006), and *c*) refer to external events or objects in the environment (e.g., Seyfarth et al. 1980). Overall however, calls of primates are still largely hardwired and tightly tied to emotional states (see for a recent review Arbib et al. 2008).

However, human children undergo a gesture phase before they use their first spoken words (Bates et al. 1975), adult speakers typically combine their verbal output with manual gestures (termed co-speech gestures, McNeill 1985), and deaf cultures develop full-fledged sign languages which function without any use of speech at all (Klima & Bellugi 1979; Stokoe 2001). Another approach to the origins of human language thus concerns the possibility that the cognitive and social-cognitive processes that underlie human language evolved in the visual-gestural modality (e.g., Condillac 1971; Hewes 1973; Hockett 1978; Armstrong et al. 1995).

The majority of studies focused on the use and function of gestures in humans (e.g., Bates et al. 1979; Kendon 1986; Iverson & Goldin-

Meadow 1998; Goldin-Meadow 2003) and provided evidence that gestures are highly iconic, spontaneously produced communicative means which are intertwined with spoken language in time (McNeill 1992). However, some human gestures are used functionally in ways very similar to language: that is, symbolically, referentially, and based on intersubjectively learned and shared social conventions (for a recent review see Pika 2008b). Gestures thus represent very complex and intriguing communicative means and current debates concern the extent to which they function as primarily communicative aids (e.g., Alibali & Don 2001; Kendon 2004), cognitive aids (e.g., as encoding or lexical access, Rime 1982; Krauss et al. 1995), or both (e.g., Bavelas 1994; Özyürek 2002; de Ruiter 2006).

However, a detailed understanding of the use and function of these communicative means in other animals might even be more useful for inferring the communicative and cognitive skills that were available at the dawn of human language. Since observations of non-vocal abilities of animals other than primates are mainly of an anecdotal nature (Lorenz 1927, 1951) or concern displays (e.g., McDonald & Potts 1994; Kotiaho 2002; Jennings et al. 2003)², the present paper will focus on the intentional and flexible use of gestures of primates only. It aims to provide an overview of the current state of the art and enables a qualitative comparison between primates and gestural abilities of pre-linguistic or just-linguistic human children. I will then elaborate on the “grooming and gossip hypothesis” proposed by Dunbar (1996) to evaluate whether this hypothesis can be applied to explain the shift from imperative to declarative signalling (Pika 2008a).

2. Non-vocal Signalling in Primates

The majority of research attention has been focused disproportionately on the great apes and less attention has been paid to the smaller apes and monkeys. Anecdotal evidence suggests that New World monkeys and

² However, Gwinner (Gwinner, E. [1964]. Untersuchungen über das Ausdrucks- und Sozialverhalten des Kolkraben [*Corvus corax corax* L.]. *Zeitschrift für Tierpsychologie* 21: 657–748) provides a very detailed overview on the expressive movements of ravens.

prosimians rely mostly on affective expressions such as pilo-erection, body postures and facial expressions (e.g., Moynihan 1967). Due to the current lack of data, the present paper will focus on non-vocal abilities of Old World monkeys and apes only.

2.1. *Early Attempts*

Early attempts to investigate gestural abilities of primates can be divided in two main domains: gestural communication with humans and gestural communication with conspecifics.

2.1.1. *Gestural Communication with Humans*

A pioneer of primate ethology and cognitive psychology was Ladygina-Kohts (1935), who provided the first comparative study of ape emotions and intelligence. This study was based on detailed descriptions of the expressive behaviour (including gestures and facial expressions) of a single-housed juvenile chimpanzee (*Pan troglodytes*), Joni, and observations of her own child, Roody, ten years later.

Hoyt (1941) raised a female gorilla (*Gorilla gorilla*), Toto, from infancy to the age of nine years in her own home and provided the first anecdotes of imperative³ *pointing* gestures (see also Yerkes 1943). Toto pointed to request desired food and liquid but used this and other gestures also in a hiding game. In this game, she would for instance hide an object (keys) under her armpit, and would then point to and show parts of her body where the object was *not* hidden, e.g. point to her elbow, open both hands, show the soles of her feet.

Interestingly, Yerkes, who stimulated much work on primate intelligence from the 1920's onward (e.g., Yerkes 1927; Yerkes & Yerkes 1929), already noticed the difference in vocal and gestural control and wrote in 1925: "I am inclined to conclude from the various evidences that the great apes have plenty to talk about, but no gift for the use of sounds to repre-

³ Imperative gestures are used to get another individual to help in attaining a physical goal: Bates, E. (1976). *Language and Context: The Acquisition of Pragmatics*. New York: Academic Press; Pika, S. (2008a). Gestures of Apes and Pre-linguistic Human Children: Similar or Different? *First Language* 28: 116–140.

sent individual, as contrasted with racial, feelings or ideas. Perhaps they can be taught to use their fingers, somewhat as does the deaf and dumb person, and thus helped to acquire a simple, nonvocal 'sign language'" (Yerkes 1925: 180). In 1966, Gardner & Gardner (1969) followed his suggestion after various attempts to teach apes spoken language had failed (e.g., Kellog & Kellog 1933; Hayes & Hayes 1951). Gardner and Gardner raised a chimpanzee female, Washoe, in a house trailer, equipped with most of the necessary items of a human environment, and social interactions with at least one human companion during the day, and taught her American Sign Language. Washoe was able to learn and use over a hundred of signs in appropriate ways and also invented new signs or altered taught signs in a purposeful way, indicating a productive gestural ability. This success led to similar projects with a gorilla, Koko (Patterson 1978b), and an orang-utan (*Pongo pygmaeus*), Chantek (Miles 1990).

Another approach to investigate primate communicative abilities was introduced by Premack (1976), who tried to overcome the speech barrier by using plastic tokens to stand for spoken words in communicating with a chimpanzee, Sarah. Furthermore, Rumbaugh (1977) created a visual language based on graphic symbols (lexigrams) depicted on a computerized keyboard for the chimpanzee, Lana. However, the most impressive results regarding human language comprehension have come from a bonobo (*Pan paniscus*), Kanzi, who acquired his first lexigrams by observing his mother, Matata, interacting with humans around a computerized keyboard and by growing up in a human enculturated environment (e.g. Greenfield & Savage-Rumbaugh 1990; Savage-Rumbaugh & Brakke 1992; Savage-Rumbaugh et al. 1998). This learning process is also apparent in human children (Lock 1978; Bruner 1983), who acquire the majority of their early linguistic abilities without explicit training but rather as a result of highly predictable, routine interactions with adults. Furthermore, Kanzi understands lexigrams as symbols in the sense that he uses them in the absence of a particular referent and in a decontextualized manner; his early vocabulary resembles that of human children.

These lines of research thus provided the first evidence that apes use gestures and ideograms intentionally and referentially, and are able to use crucial aspects of language in cases where the vocal-auditory channel can be by-passed.

2.1.2. Gestural Communication with Conspecifics

The early studies of the natural gestural communication of primates with conspecifics had their roots in the ethological tradition of cataloguing the different units of behaviour into comprehensive repertoires (Lorenz 1937; Tinbergen 1963) and mainly concerned apes. However, a few descriptions of non-vocal signals of monkeys are available.

Monkeys:

For example, Kummer (1968) investigated the social behaviour of a wild troop of hamadryas baboons (*Papio hamadryas*) in Ethiopia. He described *notifying behaviour*, in which a baboon approaches another individual and looks directly into her face. This behaviour occurs mainly when an individual leaves others in a troop and has been interpreted as an attention-getting behaviour. Similarly, baboons use a *ground-slap*, which seems also to serve as an attention-getter but also as a kind of teasing behaviour during play (Kummer & Kurt 1965).

In addition, Struhsaker (1975), who studied the behaviour of red colobus monkeys (*Piliocolobus tephrosceles*) in Uganda described a variety of non-vocal signals such as *grab* and *slap toward without physical contact*, *branch shake*, *branch-bounce*, *leaping about* and *present type II* used during display, *stare with extended forequarters* used as an aggressive threat gesture, *present* utilized as an appeasement signal and *touch* interpreted as a pacification gesture.

Apes:

The non-vocal communication of apes has received much more research attention, with the majority of studies focusing on common chimpanzees. Van Lawick-Goodall (1968b, 1968a) published the first behavioural ethogram of a chimpanzee community in Tanzania, and described over a dozen distinct gestures, used in a variety of contexts such as submission, reassurance, greeting, feeding, grooming, sex and aggression. Her work was supplemented by Plooi (1978, 1984), who was the first researcher to study the ontogeny of communicatory signals using Speech Acts Theory (Austin 1962; Searle 1969; Bates et al. 1975). Plooi showed that the onset of imperative gestures at the age of 9 and 12.5 months marks the developmental shift from acts without social-communicatory intention to intentional actions in infant chimpanzees.

Van Hooff (1973) studied the social behaviour of a captive chimpanzee group and compared his findings to those on chimpanzees observed by Van Lawick-Goodall (1968b). Interestingly, a variety of researchers describe distinct behaviours, such as *head tip* and stylized *arm raise* (Van Lawick-Goodall 1968b), *head shake* and *vacuum thrust* (Van Hooff 1973), the *grooming hand clasp* (McGrew & Tutin, 1978), and *leaf clipping* (Nishida 1980), which are absent at other study sites or groups and thus seem to provide evidence for the existence of population-specific differences in chimpanzee communities (Whiten et al. 1999).

Nishida and colleagues (1999) provided the most complete chimpanzee ethogram to date, which also includes comparisons with the behaviour of the chimpanzee's closest congener, the bonobo.

Although researchers studying the social behaviour of bonobo populations in their natural habitats describe a variety of communicative behaviours (e.g., Kano 1980; Kuroda 1980; Badrian & Badrian 1984; Ingmanson 1996), gestural abilities of bonobos were mainly investigated in detail in groups in captivity (Savage-Rumbaugh et al. 1977; Savage-Rumbaugh & Wilkerson 1978). Savage-Rumbaugh and colleagues, for instance, observed the use of 20 different gestures in the sexual context, and de Waal (1988) provided a qualitative comparison of the communicative repertoires of bonobos and chimpanzees, also including non-vocal means.

Little research attention has been focused on the non-vocal abilities of gorillas, with the first behavioural ethograms being conducted in the second half of the last century (Schaller 1963, 1965; Fossey 1974; Ogden & Schildkraut 1991). Subsequent research centred on single gestures (*clap*, Fay 1989; *splash-display*, Parnell & Buchanan-Smith 2001), but led also to a very detailed study on non-vocal signal use in a group of captive gorillas (Tanner & Byrne 1996, 1999).

In contrast to the African great ape species, substantially less is known about the gestural abilities of the Asian apes. MacKinnon (1974; but see also Rijksen 1978) provided a description of tactile and visual gestures of orangutans in their natural environment, while Ellefson (1967, 1974) studied the communicative behaviour of white-handed gibbons (*Hyllobates lar*) in the wild. A bit more research attention has been dedicated to non-vocal behaviour of siamangs (*Symphalangus syndactylus*), with

studies on wild (Chivers 1976; Palombit 1992) and captive groups (Fox 1977; Orgeldinger 1999).

2.2. *Recent Attempts*

Similar to early attempts at communication research, current studies focus on gestural abilities of primates in either interactions with humans or during their natural communication with conspecifics.

2.2.1. *Gestural Abilities in Interactions with Conspecifics*

The vast majority of research attention still concerns non-vocal signalling in apes. However, Maestriperi (1997, 1999) provided a detailed account of gestural signalling in macaques by comparing non-vocal usage in three macaque species (*Macaca mulatta*, *M. arctoides*, *M. nemestrina*). His data showed that along with group size, characteristics of a social structure, such as reduced influence of dominance and kinship, may select for a wider communicative repertoire. In addition, he described the following behaviour between mother infant dyads: When pigtail macaque mothers want their infants to follow them and the infants do not, the mothers sometimes return and stare in the infant's face (or even poke the infant) before leaving again (Maestriperi 1996).

Research on gestural abilities of apes with their conspecifics followed the lead provided by Plooi (1978, 1979, 1984) and studies on preverbal abilities of human children (Bates et al. 1975, 1979). Tomasello and colleagues (e.g., 1985, 1994, 1997a, 1997b) for instance focused on underlying processes of social cognition, including learning mechanisms and flexibility of use. Their first studies were concerned with chimpanzees in captivity only, but were later supplemented by studies on all other ape species such as bonobos (Pika et al. 2005; Pika 2007a), gorillas (Pika et al. 2003; Pika 2007b), orangutans (Liebal et al. 2006; Liebal 2007a), and siamangs (Liebal et al. 2004b; Liebal 2007b). This comparative data base enabled direct comparison of gestural abilities of all ape species in captivity and revealed that apes develop multifaceted gestural repertoires, which fall into three main sensory modalities, auditory, tactile and visual gestures (for an overview see Tomasello & Call 2007). Although like all mammals, apes have a number of more or less involuntary postural and

facial displays that express their emotional state (e.g. pilo-erection, fear grin, etc.), they use a number of gestures intentionally, that is, in flexible ways tailored for particular social circumstances. These gestures are contrary to emotional displays clearly learned (as not all individuals use them), are mechanically ineffective (in the sense that they do not function to move or manipulate the recipient's body or limbs) and solicit a voluntary response from the recipient (see also Pika 2008b). Intentional gestures fall into two categories: "attractors," which are imperative gestures aimed at getting others to look at the self, and "incipient actions" that have been conventionalized into gestures (see also Tinbergen 1951 on "intention-movements"). The underlying learning mechanism is most likely an individual learning mechanism, called conventionalization (Mead 1910, 1934; Vygotsky 1978; Bates et al. 1979; or by some authors called "ontogenetic ritualization," Tomasello & Call 1997). In this process a communicatory signal is created by two individuals shaping each others' behaviour in repeated instances of an interaction:

1. Individual A behaves intentionally toward another (e.g., an infant who wants to get carried grabs on to its mother's leg to climb up).
2. The recipient reacts in a predictable way (e.g. the mother lowers her back to allow easier access).
3. On some subsequent occasion, the recipient anticipates this sequence on the basis of its first step (e.g. the mother lowers her back at the *initial* touch of the infant).
4. The initiator learns over repetitions of this sequence to shorten its behaviour to just that initial step (e.g., *touch* leg as an intentional signal for eliciting the mother's receptivity to carrying).

In other words, a behaviour that was not at first a communicative signal becomes one as interactants anticipate each other's behaviour over time (Tomasello & Call 1997). However, Pika and colleagues (2003, 2005) also observed four group-specific gestures in a gorilla and a bonobo group. These findings are thus consistent with observations on group-specific gestures in chimpanzees in their natural habitats (e.g., Van Lawick-Goodall 1968b; Nishida 1980; Nakamura et al. 2000) and may imply that a social learning process plays an important role for the acquisition of some gestures (e.g., Carpenter & Call 2002).

Pika & Mitani (2006, 2009) used the same theoretical framework to carry out a study on gestural signalling in chimpanzees in their natural environment. First results of this long-term study provide evidence that chimpanzees use distinct gestures, so called *directed-scratches*, to refer to areas of their body to be groomed. They thus might function referentially and represent the first systematic observation of a referential gesture in the wild (for anecdotes on referential gestures in apes in the wild see also Inoue-Nakamura & Matsuzawa 1997; Vea & Sabater-Pi 1998).

Furthermore, Bard (1992) investigated the communicative abilities of orangutan infants in a food sharing context, and found that intentional produced behaviours could be observed at the age of 1–6 months, while intentional produced gestures were only used in older orangutans, ranging from 2½ to 5 years of age.

2.2.2. *Gestural Abilities in Interactions with Humans*

The ability of apes to use gestures in flexible ways has also been shown in a variety of controlled behavioural experiments. For example, Leavens and colleagues (e.g., 2004, 2005) showed that chimpanzees use imperative *pointing* gestures to direct the attention of human caretakers to food outside of their reach. Similarly, Cartmill & Byrne (2007) showed that orangutans adjust their begging gestures towards humans as a function of how well the human responds. Furthermore, Leavens and colleagues demonstrated that chimpanzees adjust their communicative behaviour according to the attentional orientation of a human experimenter. Kaminiski and colleagues (2004) provided evidence that bonobos, chimpanzees and orangutans separately take into account the body and face orientation of a human observer when using gestural signals. Liebal and colleagues (2004a) demonstrated that all four great ape species take into account the attentional state of a human experimenter, by using visual gestures preferentially when they were facing the experimenter. This study also indicated a greater sensitivity of bonobos and chimpanzees to the orientation of the human experimenter when deploying visual gestures than gorillas and orangutans; thereby uncovering a possible difference in social cognition among the great apes.

2.3. Similarities and Differences between Gestures of Apes and Prelinguistic or Just-linguistic Human Children

The above mentioned studies provided evidence that apes deploy gestures, similar to human children, as intentional acts, by operating persistently toward achieving an end state, choosing among alternative means and adjusting their use of gestures to social circumstances. These gestures are mainly of a dyadic nature, which means they are used to attract the attention of others to the self. Triadic gestures, which are used to direct the attention of the recipient to a third entity, are used less frequently, but can be found in all ape species. Examples are for instance *food begging* (i.e., an animal holds out the hand, palm up to obtain food from another, Bard 1992; Tomasello et al. 1994), *food offer* (an animal offers food placed on her arm to another one, Liebal et al. 2006), the *directed scratch* (exaggerated scratching behaviour to indicate a preferred spot on the body to be groomed, Pika & Mitani 2006), and *pointing* (Leavens et al. 1996). Differences to human children, who use both dyadic and triadic gestures from their very first attempts at gestural communication before language (Carpenter et al. 1998), are thus of a quantitative nature.

Researchers of pre-linguistic communication distinguish between three types of gestures: ritualizations, deictics, and symbolic gestures (Lock 1978; however see also Acredelo & Goodwyn 1988 for more detailed categorization). Ritualizations are gestures in which the sender uses an effective behaviour to request an action from the recipient, for instance, raising the arms to be picked up. Apes also use this type of gesture by using for instance a stylized *arm-raise* to initiate play and the supposed underlying learning process is most likely conventionalization (Pika 2008b).

Symbolic gestures represent the most sophisticated means and are communicative acts that are either associated with a referent metonymically, e.g. sniffing for a flower, or iconically, e.g. flapping the arms up and down for a flying bird (Acredelo & Goodwyn 1988). On the surface there seems to be no example of apes' gestures that bear some resemblance to symbolic gestures. Savage-Rumbaugh and colleagues (Savage-Rumbaugh et al. 1977; Savage & Bakeman 1978) and Tanner & Byrner (1996) however, describe uses of gestures of an iconic nature in two human-reared respectively nursery-reared apes. However, subsequent studies were not able to

support these findings (Roth 1995; Pika et al. 2003, 2005). The iconicity may thus only exist in the eyes of the human beholder or may be due to growing up in human enculturated environments. Pika & Mitani (2006, 2009) observed the frequent performance of so called *directed scratches* in chimpanzees in the wild, which are used to indicate certain areas on the body to be groomed. These gestures seem to share components of deictic and iconic gesture types, because they may be used to make reference and resemble the desired action, namely grooming. Although it cannot be verified whether the iconicity was indeed intended by the signaller, these gestures represent useful tools to trace the possible developmental process of a functionally based behaviour into a true symbol. There might be four possible steps:

1. Scratching represents a purely physical process by an individual to parasites or dirt and is not used in a social manner.
2. Scratching is used frequently in contexts such as conflict, frustration and anxiety (Van Lawick-Goodall 1968b) and thus represents, in addition to the physical, also a social response. It conveys information about an individual's mood and possible intentions, which can be used by recipients (Goodall 1986). This information is not intentionally directed to recipients but the behaviour functions as a communicative signal.
3. These functionally based scratches are then conventionalized (see 2.2.1.), into truly communicative means, which are intentionally produced and convey a specific meaning. They are still very similar to the original behaviour.
4. In a later step, the signal undergoes a developmental drift from iconicity to arbitrariness; a phenomenon which occurs in sign languages due to ease, smoothness and effectiveness of communication transfer (Frishberg 1979). Since the signal does not resemble the original behaviour it represents a true symbol (Bates et al. 1979).

Concerning the underlying learning process of symbolic gestures, empirically we do not know yet whether infants learn to produce them via conventionalization, via a social learning process, or via a combination of both (Lock 1978). However, it seems most likely that human children acquire symbolic gestures through a social learning process

(Bates et al. 1979; Pika 2008a). This means that the form and meaning of symbolic gestures is established by the conventions of the specific community. A similar aspect can be found in group-specific gestures of apes, which are used in different contexts at different study sites and are most likely acquired via social learning. Nishida (1980: 117) for instance described the so called *leaf-clipping*, in which “a chimpanzee picks off one to five stiff leaves, grasps the petiole between the thumb and the index finger, repeatedly pulls it from side to side while removing the leaf-blade with the incisors, and thus bites the leaf to pieces.” This behaviour is absent from the well studied chimpanzee community in Gombe, Tanzania (Goodall 1986), but members of the Kasoje group of the Mahale Mountains, Tanzania used this gesture in three distinct contexts: sex, play, and frustration. At the community of Bossou, Guinea it is mainly used during frustration and play (Sugiyama 1981). In the chimpanzee community in Tai, Ivory coast, the form of the behaviour differs slightly, because “Tai chimpanzees take the leaf blade together from both sides of the petiole between their lips and remove them in one movement, instead of repeatedly nipping small pieces” (Boesch 1995: 7). Even more interestingly, in Tai *leaf-clipping* is usually used as part of the drumming sequence of adult males, who use it at the onset of the drumming display before they start to *pant-hoot*.

Contrary to conventionalizations, which are abundant in ape gestural repertoires, and symbolic gestures, which are non-existent in ape gestural repertoires, deictics represent a more difficult type with interesting communalities. Deictics are designed to direct the recipient’s attention to outside entities and prototypes are *showing* (e.g., holding up an object to the recipient) and *pointing*. Concerning *pointing*, researchers differentiate three main motivations: a) *pointing* for imperative purposes, (e.g., to request an object, which is out of reach, Bates et al. 1975; Pika 2008b); b) *pointing* for declarative purposes, (e.g., pointing to an object to share attention in it but *not* to possess it, Bates et al. 1975; Pika 2008b); and c) *pointing* to inform another person, (e.g., of the location of an object, Liszkowski 2005). Imperative *pointing* requires conceiving the other person as an animate “agent” of action; declarative *pointing* has been defined as a means to obtain adult’s attention (“laughter, comment, smiles and eye contact, – which we have termed ‘attention’,” Bates et al. 1975: 216);

and informative *pointing* requires the provision of information mainly to benefit the recipient (Liszkowski et al. 2006). However, recent formulations of imperative and declarative communication define these modes of communication by reference to underlying psychological processes, or mental states (Baron-Cohen 1991; Tomasello et al. 2007). Baron-Cohen (1991) for example, classifies imperative communication as an attempt to influence the behaviour of a social partner and declarative communication as an attempt to influence the mind of a social partner.

However, since observational or experimental tools are not yet available to measure whether individuals, and especially those species without speech, intend to influence one's mind (Heyes 1998; Povinelli & Vonk 2003; Tomasello et al. 2003), these definitions simply deprive us of useful comparisons.

Overall, following the original definition of Bates (1975), imperative *pointing* has been observed in captive chimpanzees interacting with their human experimenters (e.g., Leavens et al. 1996, 2004) as well as human-raised or language-trained apes (e.g., Gardner & Gardner 1969; Patterson 1978a; Woodruff & Premack 1979; Miles 1990). The only anecdotal example of declarative *pointing* stems from a bonobo in the wild (Vea & Sabater-Pi 1998), who, while sitting in a tree, *pointed* to the position of two groups of human observers, who tried to hide in nearby undergrowth. The bonobo then alternated his gaze between his group members and the humans and repeated the *pointing* gesture twice while simultaneously emitting vocalizations. Anecdotal evidence for declarative deictics in the form of *showing* stems from studies on hand-raised and language-trained apes (Patterson 1978b; Savage-Rumbaugh et al. 1985; Savage-Rumbaugh 1988). Furthermore, Savage-Rumbaugh and colleagues (1998) reported that a bonobo female directed the attention of her human caretakers toward unusual sounds in the forest by looking and gesturing in that direction. While the above mentioned studies provide convincing evidence that apes are able to *point* in imperative ways, the empirical evidence on declarativeness is rather thin and relies mainly on anecdotes and interpretations.

2.4. Conclusion

A qualitative comparison of gestural abilities in human and non-human primates provides a rich source of information to gain deeper insight in the communicative and cognitive skills that were available during the dawn of human language. Both apes and pre-linguistic human children develop multifaceted gestural repertoires that consist of gestures which are clearly learned and used as intentional means to obtain a desired goal. The capacity of great apes for intersubjectivity, while differing from that of humans, is thus not negligible, and is in line with recent experiments on cognitive skills of apes, especially chimpanzees (Tomasello et al. 2003; Herrmann et al. 2007).

However, while apes use gestures in mainly dyadic interactions and for imperative purposes, pre-linguistic children go a step beyond by using some of their gestures symbolically, and to direct the attention of others for declarative purposes. The question thus arises, what triggered the shift from the use of imperative to a mere declarative use of gestures in humans? To answer this question, I will draw upon one of the most empirically grounded of the recent theories of language origins, the so-called “grooming and gossip hypothesis” (Dunbar 2004), and argue that it may be a useful tool to create an evolutionary scenario to explain the developmental shift from imperative to declarative signalling.

3. The Grooming and Gossip Hypothesis

Several theories have been proposed to explain the evolution of species differences in brain size and intelligence, but so far no consensus has emerged (Reader & Laland 2002). Ecological explanations centre around the “extractive foraging” (Parker & Gibson 1977; Gibson 1986) and “cognitive mapping” hypotheses (Milton 1988), but claims that primate ecological strategies involve more complex problem-solving are plausible only when applied to the behaviour of particular species (e.g., termite-extraction by chimpanzees and nut-cracking by *Cebus* monkeys). “Social intelligence” (social brain) hypotheses on the other hand also cite behavioural flexibility as a key factor in the evolution of enhanced brain size, but posit that complex social interaction was responsible for the selection

pressures that favoured larger brains and more complex cognitive capacities (Jolly 1966; Humphrey 1976; Byrne & Whiten 1988; Dunbar 1998). Although it is still highly debated which brain properties might explain differences in intelligence (e.g., Reader & Laland 2002; Roth & Dicke 2005), a number of studies have shown that there is a positive linear relationship between social group size and neocortex size in primates, bats, carnivores, and cetaceans (Marino 1996; Joffe & Dunbar 1997; Barton 1999, but see Connor et al. 1998 on cetaceans). But if it were only the size of social groups that mattered, wildebeest, which live in largely anonymous unstructured herds, would be wizards (Silk 2007). Therefore, brain size is also connected to the complexity of social interactions within social groups and is correlated with the frequency of coalitions, social play, tactical deception, innovation, social learning, and with the size of grooming networks that primates form (Dunbar & Shultz 2007). These latter findings inspired the “grooming and gossip” hypothesis (Dunbar 1996, 2004), which suggests that language evolved as a mechanism for bonding large social groups, enabling a much more efficient exchange of information about the state of the social networks.

A variety of factors are known to influence group size (e.g., Caraco & Wolf 1975; Chapman et al. 1995; Janson & Goldsmith 1995; Hass & Valenzuela 2002), and the most important is likely defence against predators (e.g., Terborgh & Janson 1986; Janson & Goldsmith 1995; Fleagle 1999; Hass & Valenzuela 2002). Larger groups are more effective in detecting and warding off predators than smaller groups, but sociality also exposes animals to a number of direct costs. These include, for instance, travelling greater distances in search of food in order to provide enough food per group member, which is linked with a higher exposure to predation; higher energy disturbances to feeding; harassment by more dominant individuals; and disruptive effects that coerce conspecifics to make decisions which do not always represent the most ideal solution for each animal. Sociality thus demands “compromise on one’s personal, short-term objectives so that one gains in the longer term through a greatly reduced risk of falling victim to a predator” (Dunbar 2004: 101). As a consequence of these costs, primates form alliances and intense bonds, and the underlying bonding mechanism used in most primates is grooming. Grooming among adult individuals occurs in a variety of mammal species

(e.g., Hart & Hart 1992; Stopka & Graciasova 2001), but is a phenomenon best described in primates (e.g., Manson et al. 2004; Lehmann et al. 2007; Schino & Aureli 2008). It consists of brushing and picking through the fur with fingers, mouth and toes (Van Lawick-Goodall 1968a), and ranges from self-grooming, over dyadic interactions to grooming sessions of several individuals (Goodall 1986). Grooming represents a time-consuming activity that can occupy up to 20% of the total day for some of the most social species (Dunbar 2004). Demonstrated or inferred benefits of being groomed include removal of ectoparasites (e.g., Saunders 1988; Tanaka & Takefushi 1993; Mooring et al. 1996; Zamma 2002), decrease of glucocorticoid concentrations (Crockford et al. 2007; Wittig et al. 2008), release of the hormone oxytocin, and β -endorphins (Keverne et al. 1989), which generates a sense of relaxation in the recipient (reduces signs of nervousness, e.g. scratching, Goosen 1981; heart rate reduction, Feh & de Mazieres 1993). Grooming is disproportionately concentrated in kin dyads (e.g., Gouzoules & Gouzoules 1987; Schino 2001), while grooming among non-kin dyads may be shaped by reciprocity (Trivers 1971). It has been suggested that grooming in non-kin dyads is exchanged for coalitional support (e.g., Seyfarth & Cheney 1984; Mitani et al. 2000; Watts 2000; Watts 2002; Muller & Mitani 2005), food (de Waal 1997), tolerance (Henzi & Barrett 1999), mating or information about reproductive status (Stopka & Macdonald 1999), protection against infanticide (Palombit et al. 1997) or for grooming itself (Henzi & Barrett 1999; Silk et al. 1999).

Furthermore, the time primates engage in social activities (i.e., the time spent servicing social relationships) is positively related to group size (at least among anthropoid primates), supporting the idea that individuals living in bigger groups have to spend more time servicing their social network than individuals living in smaller groups (Dunbar 1991; Lehmann et al. 2007).

Interestingly, grooming is absent in modern humans as a medium to establish and service social relationships, and Dunbar argues that this is due a dramatic increase in group size at some point in our evolutionary history (primate social groups ~ 50–80 individuals, human social network ~ 150 individuals, Dunbar 1998). The only way however, to enable the stable existence of such large groups was to develop an alternative mecha-

nism for bonding in which the available social time was used more efficiently. Dunbar (1993, 1996) suggests that language appears to fulfil that function perfectly, because it enables us to interact with several people at the same time and can be done simultaneously with most other activities. It thus represents a very efficient mean to manage time budgets (Dunbar 2004) and allows us to use time more economically than primates.

4. Imperative and Declarative Signalling in Evolutionary Perspective

Whether the theoretical framework of Dunbar (1996, 2004) provides a convincing solution to explain the evolutionary pressures on language evolution (e.g. see also, Deacon 1997; Knight 1998; Miller 2000; Wray 2002), it may be usefully employed to explain the developmental shift from a predominantly use of imperative gestures in primates to a mere combination of both imperative and declarative means in humans. The ancient medium for servicing and maintaining social relationships, grooming, represents mainly dyadic interactions (one-on-one activity). It relies already heavily on the successful exchange of communicative signals between sender and recipient to engage, disengage and change roles during grooming (Van Lawick-Goodall 1968b; Goodall 1986; Pika & Mitani, in preparation), and thus may constitute a prolific medium for the development of highly sophisticated gestures. This hypothesis seems to be supported by a trend apparent in primate grooming gestures, ranging from merely dyadic tactile signals in Old World monkeys to visual gestures in apes with a probably referential nature (Grigoréva & Deriagina 1987; Pika & Mitani 2006, in preparation). These self-referential gestures are triadic but imperative, because they are used to request direct actions in the form of grooming or role reversal during a grooming interaction (Pika & Mitani, in preparation). The increase of group size then might have led to a developmental shift from self-referential to referential gestures of an imperative nature, which still primarily functioned to serve grooming purposes. In a subsequent step and in conjunction with a cognitive arms race, declarative gestures might have emerged, representing the first step toward a new medium for bonding. The underlying bonding function of declarative gestures is supported by studies on social composition and context of declarative gestural occurrence: Declarative gestures are most fre-

quently used between individuals with already existing strong bonds (e.g., mother-infant dyads, Bates et al. 1979) or in situations of uncertainty, in which bonds just have to be formed (e.g., meeting of strangers). They are accompanied by other signals such as smiles and laughter, which are independently also mainly found in either situations of social confidence or in situations of uncertainty, and insecurity (Provine 1997; Fogel et al. 2006). Furthermore, declarative gestures enable not only the possibility to communicate about the here and now but also to communicate about absent referents and objects and events in the past. This behaviour is probably linked with an increased level of intersubjectivity that enables humans to understand other people as intentional agents, with whom they may share experience (Tomasello et al. 2005). Contrary, there is still an ongoing debate to what extent primates understand the intentional structure of behaviour and possess a “theory of mind” (Premack & Woodruff 1978; Heyes 1998; Tomasello et al. 2003; Andrews 2005; Pika & Zuberbühler 2007; Call & Tomasello 2008; Seyfarth & Cheney 2008), or “intentional stance” (Dennett 1983). In a subsequent step in the hypothetical scenario of language evolution, “gestural grooming” (in the form of imperative and declarative gestures and probably supplemented by simple sounds), was then, due to selective pressures towards improved communication clarity, superseded by “vocal grooming” (Dunbar 1996); a modality which contrary to the gestural modality had room for improvement.

References

- ACREDELO, L.P. & GOODWYN, S.W. (1988). Symbolic Gesturing in Normal Infants. *Child Development* 59: 450–466.
- ALIBALI, M.W. & DON, L.S. (2001). Children’s Gestures Are Meant to be Seen. *Gesture* 1: 113–127.
- ANDREWS, K. (2005). Chimpanzee Theory of Mind: Looking in all the Wrong Places? *Mind & Language* 20: 521–536.
- ARBIB, M.; LIEBAL, K. & PIKA, S. (2008). Primate Vocalization, Gesture, and the Evolution of Human Language. *Current Anthropology* 49: 1053–1076.
- ARMSTRONG, D.F.; STOKOE, W.C. & WILCOX, S.E. (1995). *Gesture and the Nature of Language*. Cambridge: Cambridge University Press.
- ARNOLD, K. & ZUBERBÜHLER, K. (2006). Semantic Combinations in Primate Calls. *Nature* 441: 303.
- AUSTIN, J.L. (1962). *How to Do Things with Words*. New York: Oxford University Press.

- BADRIAN, A. & BADRIAN, N. (1984). Social Organization of Pan Paniscus in the Lomako Forest, Zaire. In: R.L. SUSMAN (ed.). *The Pygmy Chimpanzee: Evolutionary Biology and Behavior*. New York: Plenum Press.
- BARD, K.A. (1992). Intentional Behaviour and Intentional Communication in Young Free-Ranging Orangutans. *Child Development* 63: 1186–1197.
- BARON-COHEN, S. (1991). Precursors to a Theory of Mind: Understanding Attention in Others. In: A. WHITEN (ed.). *Natural Theories of Mind: Evolution, Development and Simulation of Everyday Mindreading*. Oxford: Blackwell.
- BARTON, R.A. (1999). The Evolutionary Ecology of the Primate Brain. In: P.C. LEE (ed.). *Primate Socioecology*. Cambridge: Cambridge University Press.
- BATES, E. (1976). *Language and Context: The Acquisition of Pragmatics*. New York: Academic Press.
- BATES, E. et al. (1979). *The Emergence of Symbols: Cognition and Communication in Infancy*. New York: Academic Press.
- BATES, E.; CAMAIONI, L. & VOLTERRA, V. (1975). The Acquisition of Performatives prior to Speech. *Merrill-Palmer Quarterly* 21: 205–226.
- BAVELAS, J.B. (1994). Gestures as Part of Speech: Methodological Implications. *Research on Language and Social Interaction* 27: 201–221.
- BOESCH, C. (1995). Innovation in Wild Chimpanzees. *Animal Behaviour* 48: 653–667.
- BRUNER, J.S. (1983). *Child's Talk*. New York: Norton.
- BYRNE, R.W. & WHITEN, A. (1988). *Machiavellian Intelligence: Social Expertise and the Evolution of Intellect in Monkeys, Apes and Humans*. Oxford: Clarendon Press.
- CALL, J. & TOMASELLO, M. (2008). Does the Chimpanzee Have a Theory of Mind? 30 Years Later. *Trends in Cognitive Science* 12: 187–192.
- CARACO, T. & WOLF, L.L. (1975). Ecological Determinants of Group Sizes of Foraging Lions. *American Naturalist* 109: 343–352.
- CARPENTER, M. & CALL, J. (2002). The Chemistry of Social Learning. *Developmental Science* (5): 22–24.
- CARPENTER, M.; NAGELL, K. & TOMASELLO, M. (1998). Social Cognition, Joint Attention, and Communicative Competence from 9 to 15 Months of Age. *Monographs of the Society for Research in Child Development* 36: 176–179.
- CARTMILL, E.A. & BYRNE, R.W. (2007). Orangutans Modify Their Gestural Signaling According to Their Audience's Comprehension. *Current Biology* 17: 1345–1348.
- CHAPMAN, C.A.; WRANGHAM, R.W. & CHAPMAN, L.J. (1995). Ecological Constraints on Group-size: An Analysis of Spider Monkey and Chimpanzee Subgroups. *Behavioral Ecology and Sociobiology* 36: 59–70.
- CHIVERS, D.J. (1976). Communication within and Between Family Groups of Siamang (*Symphalangus syndactylus*). *Behavior* 57: 116–135.
- CONDILLAC, E.B. de (1971). *An Essay on the Origin of Human Knowledge; Being a Supplement to Mr. Locke's Essay on the Human Understanding. A Facism. Reproduction of the Translation of Thomas Nugent*. Gainesville, Florida: Scholars' facsimiles and reprints.
- CONNOR, R.C.; MANN, J. & TYACK, P.L. (1998). Social Evolution in Toothed Whales. *Trends in Ecological Evolution* 13: 228–232.

- CROCKFORD, C. et al. (2004). Wild Chimpanzees Produce Group-specific Calls: A Case for Vocal Learning? *Ethology* 110: 221–243.
- CROCKFORD, C. et al. (2007). Social Stressors and Coping Mechanisms in Wild Female Baboons (*Papio hamadryas ursinus*). *Hormones and Behaviour* 53: 254–265.
- DEACON, T.W. (1997). *The Symbolic Species: The Co-evolution of Language and the Brain*. New York: WW Norton.
- DENNETT, D. (1983). Intentional Systems in Cognitive Ethology: The “Panglossian paradigm” Defended. *Behavioral and Brain Sciences* 6: 343–390.
- DUNBAR, R.I.M. (1991). Functional Significance of Social Grooming in Primates. *Folia Primatologica* 57: 121–131.
- DUNBAR, R.I.M. (1993). Coevolution of Neocortical Size, Group Size and Language in Humans. *Behavioral and Brain Sciences* 16: 681–735.
- DUNBAR, R.I.M. (1996). *Grooming, Gossip and the Evolution of Language*. London: Faber and Faber Ltd.
- DUNBAR, R.I.M. (1998). The Social Brain Hypothesis. *Evolutionary Anthropology* 6: 178–190.
- DUNBAR, R.I.M. (2004). Gossip in Evolutionary Perspective. *Review of General Psychology* 8: 100–110.
- DUNBAR, R.I.M. & SHULTZ, S. (2007). Evolution in the Social Brain. *Science* 317: 1344–1347.
- ELLEFSON, J.O. (1967). A Natural History of Gibbons in the Malay Peninsula. Unpublished PhD dissertation, University of California.
- ELLEFSON, J.O. (1974). A Natural History of White-handed Gibbons in the Malayan Peninsula. In: D.M. RUMBAUGH (ed.). *Gibbon and Siamang*. Basel: S. Karger.
- FAY, J.M. (1989). Hand-clapping in Western Lowland Gorillas. *Mammalia* 53: 457–458.
- FEH, C. & DE MAZIERES, J. (1993). Grooming at a Preferred Site Reduces Heart Rate in Horses. *Animal Behaviour* 46: 1191–1194.
- FLEAGLE, J.G. (1999). *Primate Adaptation and Evolution*. New York: Academic Press.
- FOGEL, A. et al. (2006). Effects of Normal and Perturbed Social Play on the Duration and Amplitude of Different Types of Infant Smiles. *Developmental Psychology* 42: 459–473.
- FOSSEY, D. (1974). Observations on the Home Range of one Group of Mountain Gorillas (*Gorilla g. beringei*). *Animal Behaviour* 22: 568–581.
- FOX, G.J. (1977). *Social Dynamics in Siamangs*. Vol. 710. Anthropology. Milwaukee: The University of Wisconsin.
- FRISHBERG, N. (1979). Recent Developments in Language and Cognition: Sign Language Research. In: B. FROKJAER-JENSEN (ed.). *The Sciences of Deaf Signing*. Copenhagen: Audiologopedic Research Group: 55–70.
- GARDNER, R.A. & GARDNER, B. (1969). Teaching Sign Language to a Chimpanzee. *Science* 165: 664–672.
- GIBSON, K.R. (1986). Cognition, Brain Size and the Extraction of Embedded Food Resources. In: J.G. ELSE & P.C. LEE (eds.). *Primate Ontogeny, Cognition and Social Behaviour*. Cambridge: Cambridge University Press.
- GOLDIN-MEADOW, S. (2003). *Hearing Gesture: How Our Hands Help Us Think*. Harvard: Harvard University Press.

- GOODALL, J. (1986). *The Chimpanzees of Gombe, Patterns of Behaviour*. Cambridge, England: The Belknap Press of Harvard University Press.
- GOOSEN, C. (1981). On the Function of Allogrooming in Old World Monkeys. In: A.B. CHIARELLI & R.S. CORRUCINI (eds.). *Primate Behaviour and Sociobiology*. Berlin: Springer.
- GOUZOULES, S. & GOUZOULES, H.K. (1987). Kinship. In: D. CHENEY et al. (eds.). *Primate Societies*. Chicago: University of Chicago Press.
- GREENFIELD, P.M. & SAVAGE-RUMBAUGH, E.S. (1990). Grammatical Combination in *Pan paniscus*: Processes of Learning and Invention in the Evolution and Development of Language. In: S.T. PARKER & K.R. GIBSON (eds.). "Language" and Intelligence in Monkeys and Apes. Cambridge: Cambridge University Press.
- GRIGORÉVA, O.M. & DERIAGINA, M.A. (1987). Gestural Forms of Communication in Primates: I. Development of Gestural Communication in Ontogenesis and Phylogenesis. *Biologitscheskije Nauki* 1: 45–50.
- GWINNER, E. (1964). Untersuchungen über das Ausdrucks- und Sozialverhalten des Kolkrahen (*Corvus corax corax* L.). *Zeitschrift für Tierpsychologie* 21: 657–748.
- HART, B.L. & HART, L.A. (1992). Reciprocal Allogrooming in Impala (*Aepyceros melampus*). *Animal Behaviour* 44: 1073–1083.
- HASS, C.C. & VALENZUELA, D. (2002). Anti-predator Benefits of Group Living in White-nosed Coatis (*Nasua narica*). *Behavioral Ecology and Sociobiology* 51: 570–578.
- HAYES, K.J. & HAYES, C. (1951). The Intellectual Development of a Home-raised Chimpanzee. *Proceedings of the American Philosophical Society* 95: 105–109.
- HENZI, S.P. & BARRETT, L. (1999). The Value of Grooming to Female Primates. *Primates* 40: 47–59.
- HERRMANN, E. et al. (2007). Humans Have Evolved Specialized Skills of Social Cognition: The Cultural Intelligence Hypothesis. *Science* 317: 1360–1366.
- HEWES, G.W. (1973). Primate Communication and the Gestural Origin of Language. *Current Anthropology* 12: 5–24.
- HEYES, C.M. (1998). Theory of Mind in Nonhuman Primates. *Behavioral and Brain Science* 21: 101–148.
- HOCKETT, C.F. (1978). In Search of Jove's Brow. *American Speech* 53: 243–313.
- HOOFF, J.A.R.A.M. van (1973). A Structural Analysis of the Social Behaviour of a Semi-captive Group of Chimpanzees. In: M. VON CRANACH & I. VINE (eds.). *Social Communication and Movement, Studies of Interaction and Expression in Man and Chimpanzee*. London & New York: Academic Press.
- HOYT, M. (1941). *Toto and I*. New York: Lippincott.
- HUMPHREY, N.K. (1976). The Social Function of Intellect. In: P.P.G. BATESON & R.A. HINDE (eds.). *Growing Points in Ethology*. Cambridge: Cambridge University Press.
- INGMANSON, E.J. (1996). Tool-using Behavior in Wild *Pan paniscus*: Social and Ecological Considerations. In: A.E. RUSSON; K.A. BARD & S.T. PARKER (eds.). *Reaching into Thought: The Minds of the Great Apes*. Cambridge: Cambridge University Press.
- INOUE-NAKAMURA, N. & MATSUZAWA, T. (1997). Development of Stone Tool Use by Wild Chimpanzees (*Pan troglodytes*). *Journal of Comparative Psychology* 111: 159–173.

- IVERSON, J.M. & GOLDIN-MEADOW, S. (1998). Why People Gesture when They Speak. *Nature* 396: 228.
- JANSON, C.H. & GOLDSMITH, M.L. (1995). Predicting Group Size in Primates: Foraging Costs and Predation Risks. *Behavioral Ecology and Sociobiology* 36: 326–336.
- JENNINGS, D.J. et al. (2003). Is the Parallel Walk Between Competing Male Fallow Deer, *Dama dama*, a Lateral Display of Individual Quality? *Animal Behaviour* 65: 1005–1012.
- JOFFE, T.H. & DUNBAR, R. (1997). Visual and Socio-cognitive Information Processing in Primate Brain Evolution. *Proceedings of the Royal Society of London Series B-Biological Sciences* 264: 1303–1307.
- JOLLY, A. (1966). Lemur Social Behaviour and Primate Intelligence. *Science* 153: 501–506.
- KAMINSKI, J.; CALL, J. & TOMASELLO, M. (2004). Body Orientation and Face Orientation: Two Factors Controlling Apes' Begging Behavior from Humans. *Animal Cognition* 7: 216–223.
- KANO, T. (1980). Social Behaviour of Wild Pygmy Chimpanzees (*Pan paniscus*) of Wamba: A Preliminary Report. *Journal of Human Evolution* 9: 243–260.
- KELLOG, W.N. & KELLOG, L.A. (1933). *The Ape and the Child*. New York: McGraw-Hill.
- KENDON, A. (1986). Some Reasons for Studying Gesture. *Semiotica* 62: 3–28.
- KENDON, A. (2004). *Gesture: Visible Action as Utterance*. Cambridge: Cambridge University Press.
- KEVERNE, E.B.; MARTENSZ, N. & TUITE, B. (1989). Beta-endorphin Concentrations in Cerebrospinal Fluid of Monkeys Are Influenced by Grooming Relationships. *Psychoneuroendocrinology* 14: 155–161.
- KLIMA, E. & BELLUGI, U. (1979). *The Signs of Language*. Cambridge, Massachusetts: Harvard University Press.
- KNIGHT, C. (1998). Speech/ritual Co-evolution: A Selfish Gene Solution to the Problem of Deception. In: J. HURFORD; M. STUDDERT-KENNEDY & C. KNIGHT (eds.). *Approaches to the Evolution of Language: Social and Cognitive Bases*. Cambridge: Cambridge University Press.
- KOTIAHO, J.S. (2002). Sexual Selection and Condition Dependence of Courtship Display in Three Species of Horned Dung Beetles. *Behavioral Ecology* 13: 791–799.
- KRAUSS, R.M. et al. (1995). The Communicative Value of Conversational Hand Gestures. *Journal of Experimental Social Psychology* 31: 533–552.
- KUMMER, H. (1968). *Social Organization of Hamadryas Baboons*. Chicago: University of Chicago Press.
- KUMMER, H. & KURT, F. (1965). A Comparison of Social Behaviour in Captive and Wild Hamadryas Baboons. In: H. VAGTBORG (ed.). *The Baboon in Medical Research*. Texas: University of Texas Press.
- KURODA, S.J. (1980). Social Behavior of the Pygmy Chimpanzees. *Primates* 21: 181–197.
- KURODA, S.J. (1984). Rocking Gesture as Communicative Behavior in the Wild Pygmy Chimpanzee in Wamba, Central Zaire. *Journal of Ethology* 2: 127–137.
- LADYGINA-KOHTS, N.N. (1935). *Infant Chimpanzee and Human Child. A Classic 1935 Comparative Study of Ape Emotions and Intelligence*. New York.: Oxford University Press.

- LAWICK-GOODALL, J. van (1968a). The Behavior of Free-ranging Chimpanzees in the Gombe Stream Reserve. *Animal Behaviour Monographs* 1: 161–311.
- LAWICK-GOODALL, J. van (1968b). A Preliminary Report on Expressive Movements and Communication in the Gombe Stream Chimpanzees. In: P.C. JAY (ed.). *Primates. Studies in Adaptation and Variability*. New York: Holt, Rinehart, and Winston: 313–374.
- LEAVENS, D.A.; HOPKINS, W.D. & BARD, K.A. (1996). Indexical and Referential Pointing in Chimpanzees (*Pan troglodytes*). *Journal of Comparative Psychology* 110: 346–353.
- LEAVENS, D.A.; HOPKINS, W.D. & THOMAS, R.K. (2004). Referential Communication by Chimpanzees (*Pan troglodytes*). *Journal of Comparative Psychology* 118: 48–57.
- LEAVENS, D.A.; RUSSELL, J.L. & HOPKINS, W.D. (2005). Intentionality as Measured in the Persistence and Elaboration of Communication by Chimpanzees (*Pan troglodytes*). *Child Development* 76: 291–306.
- LEHMANN, J.; KORSTJENS, A.H. & DUNBAR, R. (2007). Group Size, Grooming and Social Cohesion in Primates. *Animal Behaviour* 74: 1617–1629.
- LIEBAL, K. (2007a). The Gestural Communication of Orangutans. In: M. TOMASELLO & J. CALL (eds.). *The Gestural Communication of Monkeys and Apes*. Mahwah, New York: Lawrence Erlbaum Associates.
- LIEBAL, K. (2007b). The Gestural Communication of Siamangs. In: M. TOMASELLO & J. CALL (eds.). *The Gestural Communication of Monkeys and Apes*. Mahwah, New York: Lawrence Erlbaum Associates.
- LIEBAL, K. et al. (2004). Great Ape Communicators Move in Front of Recipients Before Producing Visual Gestures. *Interaction Studies* 5: 199–219.
- LIEBAL, K.; PIKA, S. & TOMASELLO, M. (2004). Social Communication in Siamangs (*Symphalangus syndactylus*): Use of Gestures and Facial Expression. *Primates* 45: 41–57.
- LIEBAL, K. (2006). Gestural Communication of Orangutans (*Pongo pygmaeus*). *Gesture* 6: 1–38.
- LISZKOWSKI, U. (2005). Human Twelve-month-olds Point Cooperatively to Share Interest with and Provide Information for a Communicative Partner. *Gesture* 5: 135–154.
- LISZKOWSKI, U. et al. (2006). Twelve- and 18-month-olds Point to Provide Information for Others. *Journal of Cognition and Development* 7: 173–187.
- LOCK, A. (1978). *Action, Gesture and Symbol: The Emergence of Language*. New York: Academic Press.
- LORENZ, K. (1927). Beobachtungen an Dohlen. *Journal of Ornithologie* 75: 511–519.
- LIEBAL, K. (1937). Biologische Fragestellungen in der Tierpsychologie. *Zeitschrift für Tierpsychologie* 1: 24–32.
- LIEBAL, K. (1951). Ausdrucksbewegungen höherer Tiere. *Naturwissenschaften* 38: 113–116.
- MACKINNON, J.R. (1974). Behaviour and Ecology of Orang Utans. *Animal Behaviour* 22: 3–74.
- MAESTRIPIERI, D. (1996). Maternal Encouragement of Infant Locomotion in Pigtail Macaques (*Macaca nemestrina*). *Animal Behaviour* 51: 603–610.
- LIEBAL, K. (1997). Gestural Communication in Macaques. *Evolution of Communication* 1: 193–222.

- LIEBAL, K. (1999). Primate Social Organization, Gestural Repertoire Size, and Communication Dynamics. In: B.J. KING (ed.). *The Origins of Language: What Nonhuman Primates Can Tell*. Santa Fe: School of American Research Press.
- MANSON, J.H. et al. (2004). Time-matched Grooming in Female Primates? New Analyses from Two Species. *Animal Behaviour* 76: 493–500.
- MARINO, L. (1996). What Can Dolphins Tell Us About Primate Evolution? *Current Anthropology* 5: 81–85.
- MARKL, H. (1983). Vibrational Communication. In: R. HUBER & H. MARKL (eds.). *Neuroethology and Behavioral Physiology*. Berlin, Heidelberg, New York: Springer.
- MCDONALD, D.B. & POTTS, W.K. (1994). Cooperative Display and Relatedness Among Males in a Lek-mating Bird. *Science* 266: 1030–1032.
- MCGREW, W.C. & TUTIN, C.E.G. (1978). Evidence for a Social Custom in Wild Chimpanzees? *Man* 13: 234–251.
- MCNEILL, D. (1985). So You Think Gestures are Nonverbal? *Psychological Review* 92: 350–371.
- LIEBAL, K. (1992). *Hand and Mind*. Chicago: The University of Chicago Press.
- MEAD, G.H. (1910). Social Consciousness and the Consciousness of Meaning. *Psychological Bulletin* 7: 397–405.
- MEAD, G.H. (1934). *Mind, Self and Society: From the Standpoint of a Social Behaviorist*. Chicago: University of Chicago Press.
- MILES, H.L. (1990). The Cognitive Foundations for Reference in a Signing Orangutan. In: S.T. PARKER & K.R. GIBSON (eds.). *Language and Intelligence in Monkeys and Apes*. Cambridge: Cambridge University Press.
- MILLER, G.F. (2000). *The Mating Mind: How Sexual Choice Shaped the Evolution of Human Nature*. New York: Doubleday.
- MILTON, K. (1988). Foraging Behaviour and the Evolution of Primate Intelligence. In: R.W. BYRNE & A. WHITEN (eds.). *Machiavellian Intelligence: Social Expertise and the Evolution of Intellect in Monkeys, Apes and Humans*. Oxford: Clarendon Press.
- MITANI, J.C. et al. (1992). Dialects in Wild Chimpanzees? *American Journal of Primatology* 27: 233–243.
- MITANI, J.C.; MERRIWETHER, A.D. & ZHANG, C. (2000). Male Affiliation, Cooperation and Kinship in Wild Chimpanzees. *Animal Behaviour* 59: 885–893.
- MOORING, M.S.; MCKENZIE, A.A. & HART, B.L. (1996). Role of Sex and Breeding Status in Grooming and Total Tick Load of Impala. *Behavioral Ecology and Sociobiology* 39: 259–266.
- MOYNIHAN, M. (1967). Comparative Aspects of Communication in New World Primates. In: D. MORRIS (ed.). *Primate Ethology*. London: Weidenfeld.
- MULLER, M. & MITANI, J.C. (2005). Conflict and Cooperation in Wild Chimpanzees. *Advances in the Study of Behavior* 35: 275–331.
- NAKAMURA, M. et al. (2000). Social Scratch: Another Custom in Wild Chimpanzees? *Primates* 41: 237–248.
- NISHIDA, T. (1980). The Leaf-clipping Display: A Newly-discovered Expressive Gesture in Wild Chimpanzees. *Journal of Human Evolution* 9: 117–128.

- NISHIDA, T. et al. (1999). Ethogram and Ethnography of Mahale Chimpanzees. *Anthropological Science* 107: 141–188.
- OGDEN, J. & SCHILDKRAUT, D. (1991). Compilation of Gorilla Ethograms. Atlanta: Gorilla Behavior Advisory Group.
- ORGELDINGER, M. (1999). Paarbeziehungen beim Siamang-Gibbon (*Hylobates syndactylus*) im Zoo: Untersuchungen über den Einfluß von Jungtieren auf die Paarbindung. Münster: Schöningh.
- ÖZYÜREK, A. (2002). Do Speakers Design Their Cospeech Gestures for Their Addressees? The Effects of Addressee Location on Representational Gestures. *Journal of Memory and Language* 46: 688–704.
- PALOMBIT, R.A. (1992). Pair Bonds and Monogamy in Wild Siamang (*Hylobates syndactylus*) and White-handed Gibbon (*Hylobates lar*). Unpublished PhD-Dissertation, University of California.
- PALOMBIT, R.A.; SEYFARTH, R.M. & CHENEY, D.L. (1997). The Adaptive Value of “Friendships” to Female Baboons: Experimental and Observational Evidence. *Animal Behaviour* 54: 599–614.
- PARKER, S. & GIBSON, K. (1977). Object Manipulation, Tool Use and Sensorimotor Intelligence as Feeding Adaptations in Cebus Monkeys and Great Apes. *Journal of Human Evolution* 6: 623–641.
- PARNELL, R.J. & BUCHANAN-SMITH, H.M. (2001). Animal Behaviour: An Unusual Social Display by Gorillas. *Nature* 412: 294.
- PATTERSON, F. (1978a). Conversations with a Gorilla. *National Geographic* 134: 438–465.
- PATTERSON, F. (1978b). Linguistic Capabilities of a Lowland Gorilla. In: F.C.C. PENG (ed.). *Sign Language and Language Acquisition in Man and Ape*. Boulder, CO: Westview Press.
- PIKA, S. (2007a). The Gestural Communication of Bonobos. In: M. TOMASELLO & J. CALL (eds.). *The Gestural Communication of Monkeys and Apes*. Mahwah, New York: Lawrence Erlbaum Associates.
- PIKA, S. (2007b). The Gestural Communication of Gorillas. In: M. TOMASELLO & J. CALL (eds.). *The Gestural Communication of Monkeys and Apes*. Mahwah, New York: Lawrence Erlbaum Associates.
- PIKA, S. (2008a). Gestures of Apes and Pre-linguistic Human Children: Similar or Different? *First Language* 28: 116–140.
- PIKA, S. (2008b). What Is the Nature of the Gestural Communication of Great Apes? In: J. ZLATEV et al. (eds.). *The Shared Mind*. Amsterdam: John Benjamins Publishing Company.
- PIKA, S.; LIEBAL, K. & TOMASELLO, M. (2003). Gestural Communication in Young Gorillas (*Gorilla gorilla*): Gestural Repertoire, Learning and Use. *American Journal of Primatology* 60: 95–111.
- PIKA, S. et al. (2005). Gestural Communication in Subadult Bonobos (*Pan paniscus*): Gestural Repertoire and Use. *American Journal of Primatology* 65: 39–51.
- PIKA, S. & MITANI, J.C. (2006). Referential Gesturing in Wild Chimpanzees (*Pan troglodytes*). *Current Biology* 16: 191–192.

- PIKA, S. & MITANI, J.C. (2009). The Directed Scratch: Evidence for a Referential Gesture in Chimpanzees? In: R. BOTHA & C. KNIGHT (eds.). *The Prehistory of Language*. Oxford: Oxford University Press.
- PIKA, S. & MITANI, J.C. (in preparation). The Complexity of Gesture Use During Grooming in Chimpanzees in the Wild.
- PIKA, S. & ZUBERBÜHLER, K. (2007). Social Games Between Bonobos and Humans: Evidence for Shared Intentionality? *American Journal of Primatology* 70: 207–210.
- PLOOIJ, F.X. (1978). Some Basic Traits of Language in Wild Chimpanzees? In: A. LOCK (ed.). *Action, Gesture and Symbol*. London: Academic Press.
- PLOOIJ, F.X. (1979). How Wild Chimpanzee Babies Trigger the Onset of Mother-infant Play. In: M. BULLOWA (ed.). *Before Speech*. Cambridge: University Press.
- PLOOIJ, F.X. (1984). *The Behavioural Development of Free-living Chimpanzee Babies and Infants*. Norwood, NJ: Ablex.
- POVINELLI, D.J. & VONK, J. (2003). Chimpanzee Minds: Suspiciously Human? *Trends in Cognitive Sciences* 4: 157–160.
- PREMACK, D. (1976). *Intelligence in Ape and Man*. Hillsdale, NJ: Lawrence Erlbaum Associates.
- PREMACK, D. & WOODRUFF, G. (1978). Does the Chimpanzee Have a Theory of Mind? *The Behavioral and Brain Sciences* 1: 516–526.
- PROVINE, R.R. (1997). Yawns, Laughs, Smiles, Tickles, and Talking: Naturalistic and Laboratory Studies of Facial Action and Social Communication. In: J.A. RUSSELL & J.M. FERNANDEZ-DOLS (eds.). *The Psychology of Facial Expression Studies in Emotion and Social Interaction*, Vol. 2, *Studies in Emotion and Social Interaction*, 2nd Series. Cambridge: Cambridge University Press.
- READER, S.M. & LALAND, K.N. (2002). Social Intelligence, Innovation, and Enhanced Brain Size in Primates. *Proceedings of the National Academy of Sciences of the United States of America* 99: 4436–4441.
- RIJKSEN, H.D. (1978). *A Field Study on Sumatran Orangutans*. Wageningen: Mededelingen Landbouwhogeschool.
- RIME, B. (1982). The Elimination of Visible Behaviour from Social Interactions: Effects on Verbal, Nonverbal and Interpersonal Variables. *European Journal of Social Psychology* 12: 113–129.
- ROTH, G. & DICKE, U. (2005). Evolution of the Brain and Intelligence. *Trends in Cognitive Science* 9: 250–257.
- ROTH, R.R. (1995). *A Study of Gestural Communication During Sexual Behavior in Bonobo (Pan paniscus, Schwartz)*. PhD dissertation, University of Calgary.
- RUITER, J.P.A. de (2006). Can Gesticulation Help Aphasic People Speak, or rather, Communicate? *Advances in Speech-Language Pathology* 8: 124–127.
- RUMBAUGH, D.M. (1977). *Language Learning by a Chimpanzee. The Lana Project*. New York: Academic Press.
- SAUNDERS, C.D. (1988). *Ecological, Social and Evolutionary Aspects of Baboon (Papio cynocephalus) Grooming Behaviour*. Cornell University.
- SAVAGE-RUMBAUGH, E.S. (1988). A New Look at Ape Language: Comprehension of Vocal Speech and Syntax. In: D.W. LEGER (ed.). *Comparative Perspectives in Modern*

- Psychology, Nebraska Symposium on Motivation, vol. 35. Lincoln, NB: University of Nebraska Press.
- SAVAGE-RUMBAUGH, E.S. & BRAKKE, K.E. (1992). Linguistic Development: Contrasts Between Co-reared Pan troglodytes and Pan paniscus. In: T. NISHIDA et al. (eds.). Topics in Primatology, Human Origins, vol. 1, Topics in Primatology. Tokyo: University of Tokyo Press.
- SAVAGE-RUMBAUGH, E.S.; RUMBAUGH, D.M. & McDONALD, K. (1985). Language Learning in Two Species of Apes. *Neurosciences and Biobehavioral Review* 9: 653–656.
- SAVAGE-RUMBAUGH, E.S.; SHANKER, S.G. & TAYLOR, T.J. (1998). Apes, Language, and the Human Mind. New York: Oxford University Press.
- SAVAGE-RUMBAUGH, E.S.; WILKERSON, B.J. & BAKEMAN, R. (1977). Spontaneous Gestural Communication Among Conspecifics in the Pygmy Chimpanzee (*Pan paniscus*). In: G.H. BOURNE (ed.). Progress in Ape Research. New York: Academic Press.
- SAVAGE-RUMBAUGH, S. & WILKERSON, B. (1978). Socio-sexual Behavior in *Pan paniscus* and *Pan troglodytes*: A Comparative Study. *Journal for Human Evolution* 7: 327–344.
- SAVAGE, S. & BAKEMAN, R. (1978). Sexual Morphology and Behavior in *Pan paniscus*. In: D.J. CHIVERS & J. HERBERT (eds.). Recent Advances in Primatology, vol. 1, Behavior. New York: Academic Press.
- SCHALLER, G.B. (1963). The Mountain Gorilla, Ecology and Behavior. Chicago: University of Chicago Press.
- SCHALLER, G.B. (1965). The Behaviour of the Mountain Gorilla. In: I. DE VORE (ed.). Primate Behaviour. New York: Holt, Rinehart and Winston.
- SCHINO, G. (2001). Grooming, Competition and Social Rank Among Female Primates: A Meta-analysis. *Animal Behaviour* 62: 265–271.
- SCHINO, G. & AURELI, F. (2008). Grooming Reciprocation Among Female Primates: A Meta-analysis. *Biology Letters* 4: 9–11.
- SEARLE, J. (1969). Speech Acts: An Essay in the Philosophy of Language. Cambridge: Cambridge University Press.
- SEYFARTH, R. & CHENEY, D. (2008). Primate Social Knowledge and the Origins of Language. *Mind & Society* 7: 129–142.
- SEYFARTH, R.M. & CHENEY, D.L. (1984). Grooming, Alliances and Reciprocal Altruism in Vervet Monkeys. *Nature* 308: 541–542.
- SEYFARTH, R.M.; CHENEY, D.L. & MARLER, P. (1980). Vervet Monkey Alarm Calls: Semantic Communication in a Free-ranging Primate. *Animal Behaviour* 28: 1070–1094.
- SILK, J. (2007). Social Components of Fitness in Primate Groups. *Science* 317: 1347–1351.
- SILK, J.B.; SEYFARTH, R.M. & CHENEY, D.L. (1999). The Structure of Social Relationships Among Female Savanna Baboons in Moremi Reserve, Botswana. *Behaviour* 135: 679–703.
- STOKOE, W.C. (2001). Language in Hand: Why Sign Came Before Speech. Washington, DC: Gallaudet University Press.
- STOPKA, P. & GRACIASOVA, R. (2001). Conditional Allogrooming in the Herb-field Mouse. *Behavioral Ecology* 12: 584–589.

- STOPKA, P. & MACDONALD, D.W. (1999). The Market Effect in the Wood Mouse, *Apodemus sylvaticus*: Selling Information on Reproductive Status. *Ethology* 105: 969–982.
- STRUHSAKER, T.T. (1975). *The Red Colobus Monkey*. Chicago: The University of Chicago Press.
- SUGIYAMA, Y. (1981). Observations on the Population Dynamics and Behavior of Wild Chimpanzees at Bossou, Guinea, 1979–1980. *Primates* 22: 432–444.
- TANAKA, I. & TAKEFUSHI, H. (1993). Elimination of External Parasites (Lice) Is the Primary Function of Grooming in Free-ranging Japanese Macaques. *Anthropological Science* 101: 187–193.
- TANNER, J.E. & BYRNE, R. (1996). Representation of Action Through Iconic Gesture in a Captive Lowland Gorilla. *Current Anthropology* 37: 162–173.
- TANNER, J.E. & BYRNE, R. (1999). The Development of Spontaneous Gestural Communication in a Group of Zoo-living Lowland Gorillas. In: S.T. PARKER; R.W. MITCHELL & H.L. MILES (eds.). *The Mentalities of Gorillas and Orangutans, Comparative Perspectives*. Cambridge: Cambridge University Press.
- TERBORGH, J.W. & JANSON, C.H. (1986). The Socioecology of Primate Groups. *Annual Review of Ecological Systems* 17: 111–135.
- TINBERGEN, N. (1951). *The Study of Instinct*. New York: Oxford University Press.
- TINBERGEN, N. (1963). On Aims and Methods of Ethology. *Zeitschrift für Tierpsychologie* 20: 410–433.
- TOMASELLO, M. & CALL, J. (1997). *Primate Cognition*. New York: Oxford University Press.
- TOMASELLO, M. & CALL, J. (2007). *The Gestural Communication of Monkeys and Apes. Mahwah, New York: Lawrence Erlbaum Associates.*
- TOMASELLO, M.; CALL, J. & HARE, B. (2003). Chimpanzees Understand Psychological States – the Question Is which Ones and to what Extent. *Trends in Cognitive Science* 7: 153–156.
- TOMASELLO, M. et al. (1994). The Learning and Use of Gestural Signals by Young Chimpanzees: A Trans-generational Study. *Primates* 35: 137–154.
- TOMASELLO, M. et al. (1997a). The Ontogeny of Chimpanzee Gestural Signals: A Comparison Across Groups and Generations. *Evolution of Communication* 1: 223–259.
- TOMASELLO, M. et al. (1997b). The Ontogeny of Chimpanzee Gestural Signals. In: S. WILCOX; KING, B. & STEELS, L. (eds.). *Evolution of Communication*. Amsterdam/Philadelphia: John Benjamins Publishing Company.
- TOMASELLO, M. et al. (2005). Understanding and Sharing Intentions: The Origins of Cultural Cognition. *Behavioral & Brain Sciences* 28: 1–17.
- TOMASELLO, M.; CARPENTER, M. & LISZKOWSKI, U. (2007). A New Look at Infant Pointing. *Child Development* 78: 705–722.
- TOMASELLO, M. et al. (1985). The Development of Gestural Communication in Young Chimpanzees. *Journal of Human Evolution* 14: 175–186.
- TRIVERS, R.L. (1971). The Evolution of Reciprocal Altruism. *The Quarterly Review of Biology* 46: 35–55.

- VEA, J.J. & SABATER-PI, J. (1998). Spontaneous Pointing Behaviour in the Wild Pygmy Chimpanzee (*Pan paniscus*). *Folia Primatologica* 69: 289–290.
- VYGOTSKY, L. (1978). *Mind in Society: The Development of Higher Psychological Processes*. Cambridge, MA: Harvard University Press.
- WAAL, F.B.M. de (1988). The Communicative Repertoire of Captive Bonobos (*Pan paniscus*) Compared to that of Chimpanzees. *Behaviour* 106: 183–251.
- WAAL, F.B.M. de (1997). The Chimpanzee's Service Economy: Food for Grooming. *Evolution and Human Behavior* 18: 375–386.
- WATTS, D.P. (2000). Grooming Between Male Chimpanzees at Ngogo, Kibale National Park, Uganda. I. Partner Number and Diversity and Reciprocity. *International Journal of Primatology* 21: 189–210.
- WATTS, D.P. (2002). Reciprocity and Interchange in the Social Relationships of Wild Male Chimpanzees. *Behaviour* 139: 343–370.
- WHITEN, A. et al. (1999). Cultures in Chimpanzees. *Nature* 399: 682–685.
- WITTIG, R.M. et al. (2008). Focused Grooming Networks and Stress Alleviation in Wild Female Baboons. *Hormones and Behaviour* 54: 170–177.
- WOODRUFF, G. & PREMACK, D. (1979). Intentional Communication in the Chimpanzee: The Development of Deception. *Cognition* 7: 333–352.
- WRAY, A. (2002). *The Transition to Language*. Oxford: Oxford University Press.
- YERKES, R.M. (1925). *Almost Human*. New York: The Century Company.
- YERKES, R.M. (1927). *The Mind of a Gorilla (parts I and II)*. Genetic Psychology Monographs. Worcester, Massachusetts: Clark University.
- YERKES, R.M. (1943). *Chimpanzees: A Laboratory Colony*. New Haven: Yale University Press.
- YERKES, R.M. & YERKES, A.W. (1929). *The Great Apes*. New Haven: Yale University Press.
- ZAHAVI, A. (1987). The Theory of Signal Selection and Some of Its Implications. In: V. DELFINO (ed.). *International Symposium of Biological Evolution*. Bari: Adriatica Editrice.
- ZAMMA, K. (2002). Grooming Site Preferences Determined by Lice Infection Among Japanese Macaques in Arashiyama. *Primates* 43: 41–49.